

# Habitat-Choice Polymorphism Associated with Cryptic Shell-Color Polymorphism in the Limpet *Lottia digitalis*

by

BRUCE A. BYERS

Natural Science Program, University of Colorado, Boulder, Colorado 80309, USA

*Abstract.* *Lottia digitalis* is a common limpet of the mid- to high-intertidal zone of the Pacific coast of North America. It inhabits rock surfaces, where its shell is typically dark brown or gray in color; it is also common on the plates of the goose barnacle *Pollicipes polymerus*, where its shell is typically white with a pattern of black lines, making it extremely cryptic on this background. In a study on the central Oregon coast, *L. digitalis* living on *Pollicipes* clusters or the surrounding rock were individually marked, moved to the opposite habitat in an unfamiliar area, and observed for up to 12 days. Most limpets of both rock- and *Pollicipes*-type returned to their original habitats, so a true habitat-choice polymorphism exists. This behavioral polymorphism is associated with shell-color polymorphism in a clearly adaptive way. Evidence that selection by bird predators is acting to improve the match between shell color and habitat was obtained. Little evidence that selection is acting on habitat choice was found. Mechanisms for maintaining this adaptive association are discussed.

## INTRODUCTION

*Lottia digitalis* (Rathke, 1833) (= *Collisella digitalis*; see LINDBERG, 1986) is a common limpet of the mid- to high-intertidal zone of the Pacific coast of North America. It has a striking shell-color and pattern polymorphism that has attracted the attention of researchers for at least 40 years (TEST, 1945; GIESEL, 1970; HARTWICK, 1981; LINDBERG, 1981; MERCURIO *et al.*, 1985). Shells of this species range from pure white with no markings to dark brown, gray, or black; most have some dark stripes or patterns on a lighter ground color. Shell color and pattern vary with substratum. Limpets found on the white plates of the goose barnacle *Pollicipes polymerus* are typically white or cream colored with a pattern of black or dark brown lines or chevrons. Their color and pattern make them extremely cryptic on this background. Those found on bare rock are generally much darker and much less conspicuous than light-colored limpets would be.

Visually hunting predators of *Lottia digitalis*—birds such as black oystercatchers, surfbirds, black turnstones, and gulls (FRANK, 1982; GIESEL, 1970; HARTWICK, 1981; LINDBERG, 1981; LINDBERG *et al.*, 1987; MERCURIO *et al.*, 1985) and fish such as surfperch (LINDBERG, 1981; MERCURIO *et al.*, 1985)—may play a role in maintaining this color and pattern polymorphism.

*Lottia digitalis* exhibits homing behavior (BREEN, 1971; FRANK, 1964, 1965a, 1982; GALBRAITH, 1965; MILLARD, 1968; MILLER, 1968; VILLEE & GROODY, 1940). Experiments capable of distinguishing between homing and habitat choice require habitat reversal of marked individuals in an unfamiliar area (BYERS & MITTON, 1981). GIESEL (1968, 1970) reported that *Pollicipes*-type *L. digitalis* exhibit habitat choice, but his behavioral experiments did not rule out homing by studying habitat reversal in an unfamiliar area.

Experiments described in this report were undertaken to determine whether *Lottia digitalis* exhibits true habitat choice, to examine associations between shell color and habitat choice, and to seek evidence of changes in shell color and/or habitat choice produced by selection. Such experiments may lead to a better understanding of how the adaptive association between cryptic coloration and habitat choice is maintained.

## MATERIALS AND METHODS

This study was carried out at Middle Cove, Cape Arago, Oregon (43°19'N, 124°24'W), between 22 July and 3 August 1986. The study site in the southern part of the cove is partially protected from the west and northwest by a

Table 1  
Experimental treatment, shell color, and habitat-choice measures by cluster.

	Cluster								
	1	2	3	4	5	6	7	8	9
Tidal height of cluster (m)*	1.6	2.2	2.2	1.9	1.9	1.6	1.6	1.4	1.6
Cluster size (cm <sup>2</sup> )	210	397	265	123	99	247	213	144	303
Bird accessibility	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No
Experimental group†	MC	FAM	FAM	UNF	UNF	UNF	UNF	UNF	UNF
Number of limpets‡	32	32	32	28	16	50	50	32	64
Shell length (mm)									
P-type§: mean	9.71	11.50	10.22	10.01	11.11	10.59	10.27	9.86	10.33
SE	0.59	0.47	0.42	0.55	0.77	0.24	0.23	0.13	0.26
R-type: mean	12.45	12.04	10.48	8.99	10.39	11.05	11.94	11.34	10.99
SE	0.67	0.46	0.35	0.59	0.74	0.33	0.46	0.27	0.31
Shell-color score									
P-type: mean	3.81	3.31	3.56	4.07	3.25	3.20	4.04	3.38	4.09
SE	0.44	0.33	0.33	0.45	0.45	0.34	0.27	0.40	0.26
R-type: mean	7.63	7.75	8.06	8.36	8.25	8.24	6.40	6.81	5.97
SE	0.29	0.28	0.17	0.23	0.37	0.27	0.22	0.28	0.24
Days To Return									
P-type: mean	N.A.¶	2.80	3.35	2.00	2.44	2.26	2.66	2.25	2.58
SE		0.37	0.56	0.59	1.12	0.39	0.59	0.51	0.43
R-type: mean	N.A.	3.78	2.84	0.54	0.81	0.96	1.30	1.75	1.53
SE		0.51	0.41	0.33	0.40	0.21	0.31	0.39	0.26
Day 5 Habitat, % return									
P-type	N.A.	40	39	83	60	89	43	93	65
R-type	N.A.	100	100	100	100	95	100	100	100
Final Habitat, % return									
P-type	N.A.	46	67	80	67	92	61	100	81
R-type	N.A.	100	100	100	100	95	100	100	100

\* Approximate height, meters above M.L.L.W. (=0.0 m).

† MC = marking control; FAM = familiar-area habitat-reversal, homing control; UNF = unfamiliar-area habitat-reversal, habitat-choice experiment.

‡ One-half of each *n* are *Pollicipes*-type, one-half rock-type; does not apply to habitat-choice measures owing to incomplete recovery of marked limpets.

§ P-type = originally on *Pollicipes*; R-type = originally on rock.

¶ N.A. = not applicable.

rocky reef. The rock substratum at Middle Cove is fine-grained sandstone.

Four pairs of clusters of the barnacle *Pollicipes polymerus* were selected for limpet behavioral experiments. Clusters in each pair were at approximately the same height in the intertidal zone, and at least 3 m from the other cluster of the pair (Table 1). One additional *Pollicipes* cluster was chosen as a control for marking disturbance. Clusters were well defined, and surrounded by large areas of mostly bare rock (Figure 1). Accessibility of each cluster to avian predators of limpets was judged by whether or not there was a vertical surface where a bird could stand within 25 cm of the cluster (FRANK, 1981, 1982).

Limpets from each *Pollicipes* cluster and an equal number from the rock around it were removed from the substratum using a spatula. Limpets from the surrounding

rock were chosen arbitrarily, but some attempt was made to choose individuals from the same size range as those found on the *Pollicipes* cluster. In most cases enough limpets were found on the rock within about 30 cm of the cluster to equal the number removed from the cluster. The length of each individual—an indirect measure of age (FRANK, 1965b)—was measured to the nearest 0.1 mm using vernier calipers.

Each limpet's shell color was then scored using a system modified from GIESEL (1970) and HARTWICK (1981). The apex and rim of the shell were scored 0 for white, 1 for gray or grayish brown (or for the rim, also alternating white and dark), and 2 for brown. The shell between the apex and rim was scored 0 for plain white and 6 for solid brown; 1–5 reflected increasing amounts of dark striping on the lighter background of the shell. A total color score

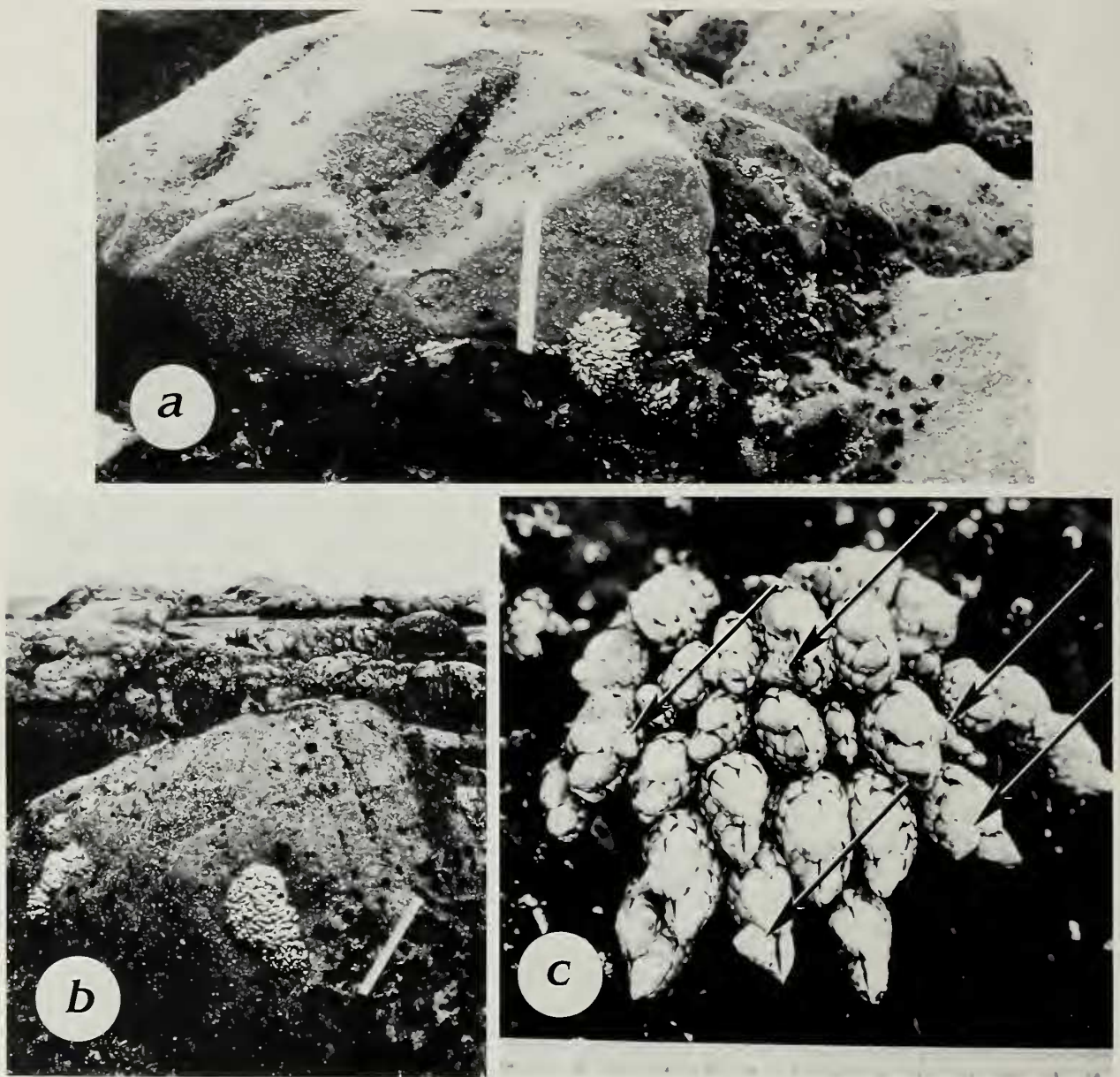


Figure 1

Representative *Pollicipes* clusters used in habitat-choice experiments (see Table 1). a. Cluster 6; ruler in photo is 30 cm long. b. Cluster 9; this cluster, on the vertical side of a large rock, had no horizontal surface within 25 cm where bird predators could stand. c. Cluster 5, with cryptic *Pollicipes*-type limpets (arrows).

was obtained by adding the apex, rim, and striping scores for each individual, such that a score of 0 represented a completely white individual, and a score of 10 a completely dark individual (Figure 2).

After measuring and color scoring each limpet, individually numbered plastic tags made for marking honeybees were glued to each shell with cyanoacrylate ester glue

(Superglue®). These numbers are durable in salt water (BYERS & MITTON, 1981).

Limpets from on or around Cluster 1, the cluster chosen as a control for disturbance due to removal, handling, and marking, were replaced in their original habitat after disturbance. One pair of clusters, Clusters 2 and 3, was chosen as a control for homing (see Table 1). Limpets originally





Figure 2

Representative shell colors and color scores (see text for details). Note numbered tags on the shells with scores 1, 4, and 6.

on *Pollicipes* in these two clusters were placed on the rock within 15 cm of their home cluster, and limpets originally on rock around these two clusters were placed on their nearby *Pollicipes* cluster. Three other pairs of clusters were used for habitat-choice experiments. Limpets originally on these *Pollicipes* clusters were placed on the rock within 15 cm of the other cluster of the pair, and thus in a completely unfamiliar habitat at least 3 m away from their home cluster. Limpets originally on rock were placed on the other *Pollicipes* cluster of the pair.

Movement of marked limpets was observed at either the morning or afternoon low tide, and on some days both. Observations were made for at least 5½ and as long as 12 days after marking. Limpets from the different clusters were marked over a period of 6 days at the beginning of the study, so they were observed for different lengths of time after marking. Habitat and position of each marked limpet was recorded as follows: individuals were noted as being on the plates of a *Pollicipes* of their home or foster cluster (the other cluster of the pair in the case of habitat reversal in an unfamiliar area), or on one of three other possible substrata—rock, the shell of a mussel *Mytilus californianus*, or a *Pollicipes* not in the home or foster cluster. If a limpet was not on the home or foster cluster, its distance from the nearest edge of the cluster was measured in centimeters. Approximately 1670 individual positions of 336 marked limpets were recorded.

These individual position records were used to analyze several aspects of habitat choice. The number of days taken to return to the original habitat, “Days To Return,” was a quantitative measure obtained for each individual. Two qualitative measures of return to the original habitat also were determined: “Day 5 Habitat” was the substratum (*Pollicipes*, rock, or mussel) of an individual either 5 or 5½ days after experimental manipulation. “Final Habitat” was a qualitative measure of whether a limpet ever returned to its original habitat after experimental reversal. In almost all cases (165/180) once a limpet returned to its original habitat it stayed there, so Final Habitat was usually the habitat on the last day of field observation.

Black oystercatchers were observed in the study area on many occasions, and on 2 August a pair was observed feeding near several study clusters. Sixteen shells of recently eaten rock-type *Lottia digitalis*, none marked, were

found approximately 60 cm from one of these clusters. These shells were scored for color.

## RESULTS

### Shell-Color Polymorphism

The shell-color distributions of limpets from the two habitats were clearly bimodal (Figure 3). *Pollicipes*-type limpets had a mean color score of 3.69 (SD = 1.52) and rock-type limpets had a mean score of 7.29 (SD = 1.45). These means differed significantly ( $t = 22.19$ ,  $df = 334$ ,  $P < 0.001$ ). The variance of shell color in each group was large, and the two groups overlapped to some extent.

### Shell-Color Change with Age and Evidence for Selection

In *Pollicipes*-type limpets (all clusters;  $n = 168$ ) there was a significant regression of shell color on length ( $b = -0.152$ ,  $SE\ b = 0.071$ ,  $F = 4.57$ ,  $P = 0.034$ ). Larger, and thus older, *Pollicipes*-type limpets were lighter than smaller, younger ones. This relationship was not significant in rock-type *Lottia digitalis* (all clusters;  $n = 168$ ;  $b = -0.007$ ,  $SE\ b = 0.054$ ,  $F = 0.018$ ,  $P = 0.892$ ).

Color scoring of the shells of 16 rock-type limpets eaten by black oystercatchers allowed a direct test, although with a very small sample, of whether the shell color of limpets eaten by predators differed from the mean color of limpets in the same area. A  $t$ -test showed no significant difference between the eaten limpets and the population average.

Comparison of the shell color of limpets from clusters that differed in accessibility to bird predators (Table 1) showed that rock-type limpets found around Cluster 9, the only cluster not accessible to birds, were significantly lighter in color than those from all other clusters ( $t = 7.4$ ,  $df = 159$ ,  $P < 0.001$ ). No significant shell-color difference between limpets from clusters accessible or not accessible to birds were found in *Pollicipes*-type limpets ( $t = 1.80$ ,  $df = 159$ ,  $P = 0.073$ ), but limpets from the cluster accessible to birds had the darkest shells of any cluster (Table 1).

### Habitat Choice

Limpets showed highly significant return to their original habitats from both familiar-area habitat-reversal ex-

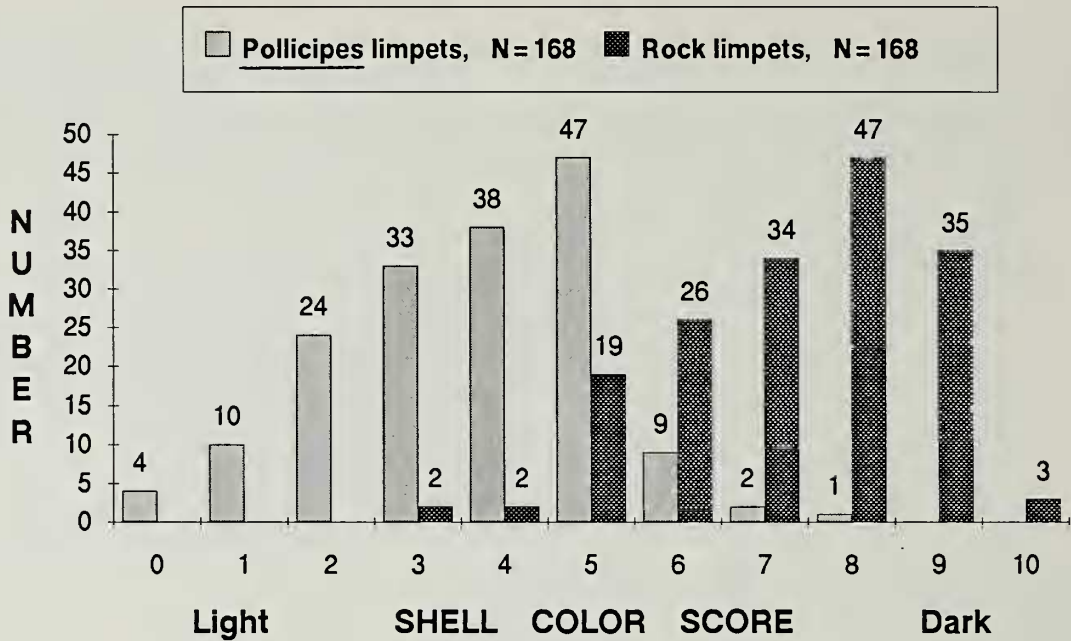


Figure 3

Frequency distribution of the shell-color scores for *Pollicipes*-type and rock-type limpets ( $n = 336$ ).

periments (Table 2) and unfamiliar-area reversal experiments (Table 3). Limpets in the marking-control cluster, Cluster 1, were not observed in a habitat other than their original habitat.

*Pollicipes*-type limpets from the two familiar-area habitat-reversal clusters returned to their original habitats at a significantly lower frequency than those from the six

unfamiliar-area reversal clusters. This difference was significant both for Day 5 Habitat ( $\chi^2 = 7.40$ ,  $df = 1$ ,  $P = 0.007$ ) and Final Habitat ( $\chi^2 = 4.90$ ,  $df = 1$ ,  $P = 0.023$ ) measures. Essentially all rock-type limpets from both familiar- and unfamiliar-area reversal experiments returned to their original habitat. Because *Pollicipes*-type limpets from familiar- and unfamiliar-area reversal experiments

Table 2

Habitat choice after experimental reversal in a familiar area.

	Original habitat		
	<i>Pollicipes</i>	Rock	
Day 5 Habitat			
<i>Pollicipes</i>			
%	39.1	0	
$n$	9	0	
Rock			$\chi^2 = 8.84$
%	60.9	100	$df = 1$
$n$	14	23	$P < 0.01$
Final Habitat			
<i>Pollicipes</i>			
%	57.7	0	
$n$	15	0	
Rock			$\chi^2 = 21.98$
%	42.3	100	$df = 1$
$n$	11	32	$P < 0.001$

Table 3

Habitat choice after experimental reversal in an unfamiliar area.

	Original habitat		
	<i>Pollicipes</i>	Rock	
Day 5 Habitat			
<i>Pollicipes</i>			
%	73.0	1.4	
$n$	54	1	
Rock			$\chi^2 = 74.18$
%	27.0	98.6	$df = 1$
$n$	20	68	$P < 0.001$
Final Habitat			
<i>Pollicipes</i>			
%	80.8	1.0	
$n$	84	1	
Rock			$\chi^2 = 127.51$
%	19.2	99.0	$df = 1$
$n$	20	96	$P < 0.001$

differed in habitat choice, all of the following analyses of habitat choice were done using data from the six unfamiliar-area reversal clusters only, in which habitat choice was not confounded with homing.

Tables 2 and 3 show that *Pollicipes*- and rock-type limpets differ in habitat preference, but in order clearly to demonstrate habitat choice by both types of limpets, their observed distributions were compared with distributions expected from random movement in an environment with the proportions of *Pollicipes* and rock substrata found at the study site. The *Pollicipes* clusters used in the study had an average area of 222 cm<sup>2</sup> (see Table 1), and *Pollicipes*-type limpets were placed on rock within 15 cm of a *Pollicipes* cluster in habitat-reversal experiments. In a circle centered on an average cluster and extending 15 cm from its edge, there would therefore be 1498 cm<sup>2</sup> of rock substratum (87% of the total area), and 222 cm<sup>2</sup> of *Pollicipes* substratum (13% of the total area) available to limpets. *G*-tests of independence (SOKAL & ROHLF, 1969) showed that the distributions of both types of limpets differed significantly from expected distributions produced by random movement in an environment with these proportions of available substrata (*Pollicipes*-type, Day 5 Habitat:  $G = 57.48$ ,  $df = 1$ ,  $P < 0.001$ ; *Pollicipes*-type, Final Habitat:  $G = 103.66$ ,  $df = 1$ ,  $P < 0.001$ ; rock-type, Day 5 Habitat:  $G = 7.86$ ,  $df = 1$ ,  $P < 0.01$ ; rock-type, Final Habitat:  $G = 13.00$ ,  $df = 1$ ,  $P < 0.001$ ).

*Pollicipes*- and rock-type limpets differed significantly in Days To Return, the speed of return to their original habitat. Rock-type limpets returned to their original habitat with a mean of 1.22 days (SD = 1.41,  $n = 120$ ), and *Pollicipes*-type limpets with a mean of 2.41 days (SD = 2.39,  $n = 120$ ). The variance of Days To Return differed significantly between these two groups ( $F = 2.89$ ,  $P < 0.001$ ), but sine-transformed data had equal variances, and a *t*-test on these transformed data also revealed a highly significant difference between means ( $t = 3.99$ ,  $df = 238$ ,  $P < 0.001$ ).

*Pollicipes*-type limpets were much more likely to be found on rock than rock-type limpets were to be found on *Pollicipes*. Fifteen of the 120 *Pollicipes*-type limpets shifted to rock after returning to *Pollicipes*, whereas none of the 120 rock-type limpets shifted to *Pollicipes* after returning to rock. The percentage of all position records (after Day 0, the day of reversal) of *Pollicipes*-type limpets on rock was 19.3% (134/694 records); for rock-type limpets on *Pollicipes* this percentage was 7.0% (39/556 records). A *G*-test of independence showed this to be a highly significant difference ( $G = 767.0$ ,  $df = 1$ ,  $P < 0.001$ ). The percentage of individuals in each group that ever used the opposite habitat as a substratum (after Day 0) were 66.6% (80/120) of *Pollicipes*-type limpets and 21.6% (26/120) of rock-type limpets. This difference was highly significant ( $G = 51.23$ ,  $df = 1$ ,  $P < 0.001$ ).

Behavioral data also revealed that rock- and *Pollicipes*-type limpets differed in their use of mussels as alternative

substrata. Sixteen of the 120 *Pollicipes*-type limpets shifted to mussels after returning to *Pollicipes*, whereas only one of the 120 rock-type limpets shifted to mussels after returning to rock. The percentage of all position records (after Day 0) of *Pollicipes*-type limpets on mussels was 8.9% (62/694 records); for rock-type limpets this percentage was 1.6% (9/556 records). This difference was highly significant ( $G = 35.31$ ,  $df = 1$ ,  $P < 0.001$ ). This measure may be biased by mussel-prone individuals; the 62 records for *Pollicipes*-type limpets, for example, were among only 35 individuals. A way to overcome this bias is to compare the percentage of individuals in the two groups that ever used mussels as a substratum: 29.2% (35/120) of *Pollicipes*-type and 6.7% (8/120) of rock-type limpets used mussels, a highly significant difference ( $G = 22.00$ ,  $df = 1$ ,  $P < 0.001$ ).

#### Habitat-Choice Change with Age and Evidence for Selection

To test the hypothesis that the habitat-choice behavior of the limpet population changes within a generation, Days to Return was regressed against shell length, an indirect measure of age. This regression was not significant for either *Pollicipes*-type ( $b = -0.119$ , SE  $b = 0.155$ ,  $F = 0.592$ ,  $P = 0.443$ ) or rock-type limpets ( $b = 0.035$ , SE  $b = 0.065$ ,  $F = 0.286$ ,  $P = 0.594$ ).

Similarly, no differences in shell length were observed between limpets that returned or did not return for Final Habitat in either *Pollicipes*- or rock-type limpets. A significant difference in lengths was observed, however, between *Pollicipes*-type limpets that returned or did not return by Day 5 ( $t = 2.27$ ,  $df = 71$ ,  $P = 0.026$ ); limpets that did not return were significantly larger than those that did. No such difference was observed for rock-type limpets.

Partial correlation analysis revealed a significant partial correlation in rock-type limpets between shell color and Days To Return when length was controlled ( $r = -0.184$ ,  $df = 117$ ,  $P = 0.023$ ): darker rock-type limpets returned to rock faster than lighter ones did. No such correlation was observed in *Pollicipes*-type limpets ( $r = -0.058$ ,  $df = 117$ ,  $P = 0.267$ ), however.

Because virtually all rock-type limpets returned to their original rock habitat, comparisons of shell color between returnees and non-returnees were not meaningful. Among *Pollicipes*-type limpets, which returned to their original habitat less frequently, *t*-tests showed no significant differences in shell color of returnees versus non-returnees for either Day 5 Habitat ( $t = 0.75$ ,  $df = 71$ ,  $P = 0.455$ ) or Final Habitat ( $t = 1.31$ ,  $df = 102$ ,  $P = 0.192$ ).

Chi-squared tests showed no differences between either *Pollicipes*- or rock-type limpets from clusters accessible or inaccessible to birds in either Day 5 Habitat or Final Habitat. Hence, bird predation did not appear to be acting as a selective agent to change behavior.



## DISCUSSION

### Shell-Color Selection

The shell-color polymorphism observed here in *Lottia digitalis* has been reported in other studies (GIESEL, 1970; HARTWICK, 1981). If predation were responsible for this polymorphism, the frequency of cryptic limpets on each substratum should increase with age, as predators remove the more conspicuous individuals. Larger, and presumably older, *Pollicipes*-type limpets in this study were lighter, as predicted by the shell-color selection hypothesis. However, shell color may also become lighter with age because of diet or infection by shell-eroding fungus. The latter might be especially important for *Pollicipes*-type limpets, because the barnacles may provide a source of fungal infection (D. Lindberg, pers. comm.).

Shell color did not vary with shell length in rock-type limpets, contrary to the prediction of the selection hypothesis, although GIESEL (1970) did report such a correlation in a population of very small (3.0–5.9 mm) rock-type limpets.

HOAGLAND (1977) found that matching with a cryptic substratum improved with age in the gastropod *Crepidula convexa*, and HUGHES & MATHER (1986) found age-related changes in the shell colors of *Littorina* sp. living on mangroves. Predation was proposed as the cause of the shell-color changes in both studies.

The significantly lighter shell color of rock-type limpets found around the only *Pollicipes* cluster in this study that was inaccessible to bird predators suggests that bird predation affects the distribution of shell color. Avian predators appear to affect the frequency of cryptic morphs of the limpet *Scurria variabilis* in central Chile (HOCKEY *et al.*, 1987).

The rock-type limpets eaten by black oystercatchers in this study were not significantly different in color from the rest of the population. HARTWICK (1981) studied shell-color selection by black oystercatchers in limpets placed in artificial arrays in the field. The rock-type *Lottia digitalis* eaten from these arrays appear to be lighter than those in the surrounding rock-type population (HARTWICK, 1981: compare figs. 6 and 8b), as predicted by the shell-color selection hypothesis.

MERCURIO *et al.* (1985) conducted field experiments that revealed that light-colored limpets disappeared more rapidly from dark-colored mussels than from the light-colored barnacles after exposure to predation by surfperch. In addition, after exposure to bird predation, significantly more limpets disappeared from barnacles than from mussels, an unexpected result; but significantly fewer light-colored *Lottia digitalis* than dark-colored *L. pelta* (Rathke, 1833) disappeared from the barnacle substratum. The disappearance rates due to predation reported in the study by MERCURIO *et al.* (1985) are remarkably high. About 17% of *L. digitalis* on the barnacle substratum and 54% on the mussel substratum disappeared after exposure to

surfperch predation during only one high tide; about 10–20% disappeared after exposure to bird predation during one low tide. These high rates of predation suggest that selection by visually hunting predators could be strong.

REIMCHEN (1979) observed differential predation by blennies on two shell-color morphs of *Littorina maria* that occupied two different habitats; in each of which one of the morphs was cryptic.

Shell color in archaeogastropods may be affected by environmental factors, especially diet (ROBERTSON, 1985). Shell color and pattern in species of other gastropod orders has been shown to be genetically determined (CAIN & SHEPPARD, 1954; KOMAI & EMURA, 1955; PALMER, 1984, 1985; REIMCHEN, 1979). GIESEL (1970) concluded that genetic factors were the major determinant of shell color in *Lottia digitalis*, but that color could also be modified by environmental factors. Laboratory studies by D. Lindberg and J. Pearse (D. R. Lindberg, pers. comm.) suggest that shell color in this species can be modified by diet.

### Habitat Choice versus Homing

Habitat choice could play a major role in maintaining a polymorphism such as the shell-color polymorphism in this species, according to theoretical models (HEDRICK *et al.*, 1976; POWELL & TAYLOR, 1979). GIESEL (1968, 1970) reported that *Pollicipes*-type *Lottia digitalis* exhibit habitat choice. *Lottia digitalis* is known to home, however, and because Giesel's study did not include habitat reversal in an unfamiliar area, homing and habitat choice were confounded.

The results presented above conclusively demonstrate that *Lottia digitalis* has a habitat-choice polymorphism. Both *Pollicipes*-type and rock-type limpets whose habitats were reversed in an unfamiliar area showed significant return to their original habitat. Whereas rock-type limpets exhibit virtually complete fidelity to rock, not all *Pollicipes*-type limpets return to *Pollicipes*. Because the area of rock in the vicinity of an isolated *Pollicipes* cluster is much greater than the area of the cluster, the fact that most *Pollicipes*-type limpets do return to *Pollicipes* is evidence of a strong habitat preference. The slower and less complete return by *Pollicipes*-type limpets may result from the greater difficulty of finding a small, isolated *Pollicipes* cluster in a large expanse of rock.

Rather unexpectedly, *Pollicipes*-type limpets whose habitats were reversed in a familiar area returned at a significantly lower frequency than those in an unfamiliar area. A combination of homing and habitat choice in the familiar-area reversal groups should have led to a greater return frequency than habitat choice alone in the unfamiliar-area reversal groups. This difference in return rates may be due to subtle and unrecognized ecological differences between the two familiar-area reversal clusters and the six unfamiliar-area reversal clusters. It could also be that limpets are somewhat familiar with local topography, and if they are displaced and recognize some cues, they

try to return home; however, if they are displaced to a totally unfamiliar area, they switch behavioral modes and make use of habitat choice to find the nearest *Pollicipes* cluster. At the least, this result suggests that homing is not overwhelmingly strong.

#### Natural Selection for Habitat Choice

Because habitat choice is adaptively associated with shell color, the selection hypothesis would predict that differential predation would also act to improve this behavior. However, no evidence of selection acting directly on habitat choice was found: the frequency of returnees did not increase with increasing size, and none of the habitat-choice measures differed between bird-accessible and bird-inaccessible clusters.

Partial correlation analysis did show a significant correlation in rock-type limpets between shell color and Days To Return when length was controlled, however. The negative correlation coefficient ( $r = -0.184$ ) indicates that lighter rock-type limpets, which are presumably less cryptic on rock and more cryptic on *Pollicipes*, take significantly longer to return from *Pollicipes* to rock, as predicted if selection has acted to create a correlation from an initially independent distribution of shell color and behavior. In *Pollicipes*-type limpets there was no significant partial correlation between color and Days To Return when length was controlled. GIESEL (1968, 1970) reported that shell color and return time are correlated in small (<8 mm) *Pollicipes*-type limpets.

Habitat choice may be heritable, but evidence is lacking and would be difficult to obtain. Evidence for a genetic correlation between habitat choice and a fitness-related character in an insect was reported by VIA (1986). The kind of rigorous genetic analysis required to demonstrate genetic covariance between shell color and habitat choice probably would be impossible in *Lottia digitalis*, which spawns and has planktonic larvae (FRITCHMAN, 1961; GEISEL, 1970; MERCURIO *et al.*, 1985).

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#### LITERATURE CITED

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